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# THE MECHANISM OF EVOLUTION
# IN THE LIGHT OF HEREDITY AND DEVELOPMENT[1]

## II

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### 3. *The Germplasm Theory*

The germplasm theory of Weismann substitutes a simple and rational conception for this complicated and inverted view of development, heredity and evolution. According to Weismann the intrinsic causes of development are in the germplasm and not in the soma of the developed organism; the germplasm is continuous from generation to generation and is not made anew in each generation by the soma; the germplasm is relatively stable as compared with the somatoplasm, so that while the latter undergoes many changes in response to environmental stimuli, the former undergoes few. Heredity is the transmission of parental germplasms to offspring, usually through the male and female sex cells; ontogeny is the conversion of portions of the protoplasm into the differentiated tissues of the developed organism, while other portions remain unchanged, especially in the sex cells; evolution consists primarily in the transmutation of one type of germplasm into another, not of one type of developed organism into another. Thus at one stroke the germplasm theory, if accepted, eliminates most of the older theories of evolution and substitutes in the place of mysterious and even mystical causes relatively simple and mechanical ones.

Shortly after the publication in 1892 of Weismann's book on the "Germplasm" there was a general outcry against the highly speculative character of this theory. It was said that whereas genuine progress in science depends upon the control of the scientific imagination by the brake of observation and experiment, Weismann had allowed his imagination to run wild without any brake at all. One critic (Ryder) said that there was no more evidence for the existence of a germplasm separate and distinct from the body plasm than for the existence of "bowlegged hobgoblins on the back side of the moon," while another critic (Romanes) asserted that Weismann's analysis of the germplasm into units of seven different orders, such as *biophores, determinants, ids,* etc., had no more basis in reality than Dante's seven circles of the Inferno.

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[1] William Ellery Hale Lectures before the National Academy of Sciences, Washington, April 16 and 18, 1917.

Nevertheless, in spite of the general outcry against it the germplasm theory is to-day more widely accepted than ever before and all recent work on heredity and evolution confirms the essential features of Weismann's theory. Relatively minor details of the original theory have been modified or abandoned as the result of further work, but its main foundations stand fast. Among the important confirmations of the germplasm theory may be mentioned the great mass of work on Mendelian inheritance and germinal factors, while an important corollary of this theory is Johannsen's suggestive distinction of *Phenotype* and *Genotype,* the former being the developed type or soma, the latter the hereditary type or germplasm.

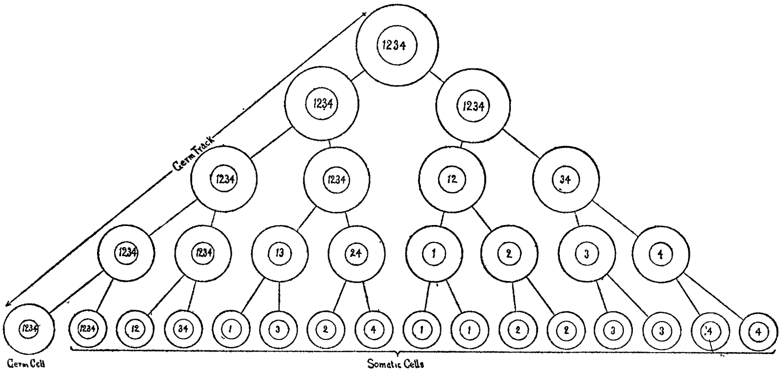

FIG. 9. *Diagram of the Mechanism of Ontogeny according to Weismann.* The determinants in the nucleus (1, 2, 3, 4) are supposed to be distributed differentially to the various somatic cells, whereas they are all found in the germ cells.

In one respect at least Weismann's theory was probably wrong and this was in the supposed manner in which the hereditary germplasm presides over development. Differentiation, according to Weismann, is caused by the disintegration of the germplasm, portions of it going into one cell and other portions into other cells, which cells differentiate into various kinds of tissue cells, depending upon the portions of the germplasm which they receive (Fig. 9). But there is no satisfactory evidence of

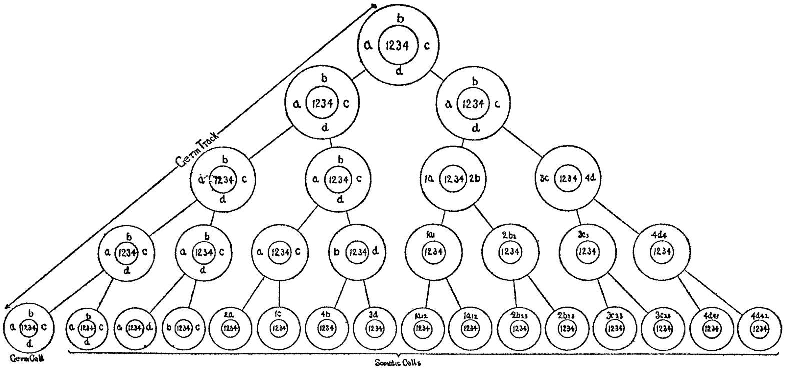

FIG. 10. *Diagram of the Mechanism of Ontogeny according to recent Workers.* The determinants or genes (1, 2, 3, 4) are distributed equally to every cell, but the cytoplasm is distributed differentially (segregation). The same determinants acting upon different cytoplasms produce different results in various somatic cells (new formation).

the qualitative division of the germplasm while the causes of differentiation may be explained in another way, as we shall see when we come to consider the mechanism of development, and as is indicated in Fig. 10.

*Germplasm Identical with Chromatin, Somatoplasm with Cytoplasm.*—The germplasm is not a mere logical abstraction; its distinctness from somatoplasm, its relatively great stability, its continuity from cell to cell, from generation to generation, from species to species are not unsupported hypotheses. We have within every cell two substances which possess these different qualities of germplasm and somatoplasm, as Hertwig, deVries, Roux, Weismann and many others have pointed out. There is convincing if not conclusive evidence that the germplasm is located mainly or entirely within the chromatin of the nucleus, while the somatoplasm, or that portion of the protoplasm which undergoes differentiation into the various structures, tissues, and organs of the developed body is the cytoplasm or substance of the cell body. Osborn (1915) accordingly calls the former of these the "heredity-chromatin," but it seems to me preferable to preserve the time-honored and familiar designations which have hitherto been used; accordingly in these lectures germplasm is thought of as located in or as identical with the chromosomes of the nucleus, while somatoplasm is located largely in the cytoplasm.

Not only is it possible to give the germplasm a cellular "habitation and a name," but it is possible to trace it from cell to cell, and from generation to generation and thus to establish its continuity; it is possible to show that the chromatin is more stable than the cytoplasm, that it comes in approximately equal quantities from both parents and that it is distributed equally to every cell of the developing organism; it is known that the quantity of this germplasm which goes into every mature egg or sperm cell is reduced to one half that found in the other cells of the body and that when egg and sperm unite in fertilization the normal quantity is again restored, and it is known that by means of this reduction and by the subsequent union of the sex cells in fertilization new combinations of germplasms are produced.

Through the work of Morgan and his pupils we are now beginning to understand something about what Weismann called "the architecture of the germplasm" and indications are at hand of the way in which this germplasm controls the differentiations of the egg and hence the development of inherited characters; and while we know little or nothing as to the precise manner in which the germplasm undergoes evolutionary changes no one acquainted with the evidence doubts that evolution can take place only through changes in the germplasm.

### 4. *The Causes of Development*

It is interesting and somewhat depressing to observe within what narrow limits the minds of men move in dealing with any great problem like that of the causes of development, whether of ontogeny or phylogeny. The modern investigator arrives at some conclusion which seems to him new and "epoch-making" only to find as he traces his discovery to its sources that it is merely a variant on some old, well-recognized theme, or in the language of modern biology a mere "fluctuation," and not a "mutation." There is nothing wholly new under the sun even in our theories, and yet there is development of ideas and evolution of theories. The outlines of the truth have long been known, but recent work has supplied many details.

Within the realm of scientific, that is of mechanistic, causation two general methods of explaining organic development, whether of a species or of an individual, have been proposed. The one finds the causes of such development in the environment, the other within the organism itself.

(*a*) *Environmental Causes of Development.*—Formerly great emphasis was placed upon the influence of environment in both ontogeny and phylogeny. The theory of epigenesis held that the distinctive causes of development were to be found in external forces and conditions rather than in the germ cells, which were supposed to be very simple in organization and practically without differentiation: and while no one now maintains, as St. Hilaire once did, that environmental conditions may determine whether an egg will develop into a reptile or a bird, it is still popularly supposed that stature is caused by the quantity and quality of food, sex by food or temperature, mentality by education, and that in general individual peculiarities are due to environmental differences.

From the earliest times it has been believed that one species might be transmuted into another by environmental changes and that even life itself might arise from lifeless matter through the influence of extrinsic conditions. The organism was regarded as being passively moulded by outside forces. Thus the theories of evolution of Buffon, Lamarck, St. Hiliare and to a certain extent of Darwin also were based upon the direct or indirect influence of environment in causing evolution. The sharp contrast which exists in certain respects between the two systems known as Lamarckism and Darwinism does not concern the influence or non-influence of environment in causing changes in organisms. Lamarck held that individual *adaptations* occur in response to environment and that these adaptations are inherited and thus become the building materials of evolution, but he did not attempt a mechanistic explanation of individual adaptations themselves. Darwin held that *variations* arise chiefly through changes in environment—"Variations of every sort," he said, "are caused by changed conditions of life"—unfavorable variations are eliminated by the environment while adaptive ones persist. Thus Darwinism offers a mechanistic explanation of adaptations, but it does not explain how changes in environment cause variations. The distinction between Lamarckism and Darwinism is to be found, therefore, in the manner in which adaptations are supposed to arise rather than in the causes of variation, for in both systems variations are usually attributed to environmental causes.

(*b*) *Intrinsic Causes of Development.*—Recent work on ontogeny and phylogeny places greater weight upon intrinsic than upon extrinsic factors in development. Modern studies of development have demonstrated the overwhelming importance of heredity as compared with environment; indeed it is doubtful whether environment serves in any other way than to hasten or retard, to stimulate or inhibit certain developmental responses of the organism, while the character and kind of response, the possibilities and limitations of development are determined by the organism itself.

In similar manner it is held by many geneticists that the distinctive or differential causes of evolution lie within the organism, and that environment plays a wholly subsidiary part. The real problem here is as to the causes of heritable variations, for it is universally recognized that these and these alone constitute the building materials of evolution. Certainly most of the variations which are caused by environment are not inherited and at present no unequivocal cases are known in which somatic variations caused by environmental change are known to be inherited.

Non-heritable variations are usually if not invariably caused by environmental changes, but many students of heredity maintain that heritable variations are always due to intrinsic or constitutional causes. Just as the constitution of the fertilized egg determines the nature of the organism which develops from it, so the constitution of the germplasm determines the nature of the heritable variations which arise from it. Davenport says, "As the egg develops into the complex adult with multitudes of differentiated cells, so primitive germplasm has developed into all present and past organisms." But this does not signify that everything which appears in the course of ontogeny or phylogeny was actually or "factorially" present in the egg or in the primitive germplasm. Development is not merely a "sorting-out process" but also a creative one. Everything which comes out of an egg or out of primitive germplasm was *potentially* in it or it could never have come out of it, but such an "explanation" of ontogeny or of phylogeny does not really explain anything. In similar manner it might be affirmed that the entire world, living and non-living, was *potential* in the material from which the world was made, without leaving us any the wiser.

Overemphasis upon the intrinsic causes of evolution and neglect of the extrinsic causes has led to the extreme view that elementary species, pure lines, unit characters or inheritance factors are immutable, except that in some instances they may undergo digressive changes like those of the radium atom, which changes are wholly independent of environment. According to this view "The foundation of the organic world was laid when a tremendously complex molecule capable of splitting up into a vast number of simpler vital molecules was evolved"

(Davenport, 1916), and evolution consists merely in "the unpacking of an original complex" (Bateson, 1914) so that it is a process of devolution, or simplification. According to this bizarre view, man would be, as Castle has said, "a simplified ameba." Such an extreme position is not unlike the "palingenesis" of Bonnet and might properly be called "natural creation" rather than "evolution," for as Caullery says, "there is no considerable difference between such views and creationist ideas."

(*c*) *Epigenesis and Endogensis.*—In the field of ontogeny no one now maintains the extreme view either of epigenesis or of preformation. The germ cells are not unorganized and wholly undifferentiated as Wolff maintained, nor do they contain a preformed organism as Bonnet taught. Development is not the creation of organization by outside forces nor is it the unfolding of an infolded organism.

> "We should look upon the germ as a living thing, and upon development as one of its functions. Just as the character of any function is determined by the organism, though it may be modified by environment, so the character of development is determined by heredity, that is by the organization of the germ cells, though the course and results of development may be modified by environmental conditions" (Conklin, 1915).

In similar manner most students of phylogeny maintain that evolution is the result of both extrinsic and intrinsic causes, of environmental and organismal factors. In the words of Darwin,

> "Although every variation is either directly or indirectly caused by some change in the surrounding conditions, we must never forget that the nature of the organization acted upon essentially governs the results."

(1) *Environment and Heredity.*—Differentiation and variation are conditioned by the organism and by the environment, by intrinsic and by extrinsic causes. In general the direction and character of individual development are determined by the organism, that is by heredity, while environment exercises a stimulating, inhibiting or modifying influence on the organism. It is altogether probable that the general factors of evolution are precisely the same as those of individual development, namely heredity and environment, and that their method of acting is the same, namely *the general direction and course of evolution is determined by the organism while environment serves merely as a stimulator, inhibitor or modifier.*

However, this contrast of organism and environment is by no means as simple and clear cut as is usually assumed. In many cases it is not only difficult to decide whether the differential cause of a character is one or the other of these, but it is even difficult to define what is meant by these two terms. The organism is not everything which lies within the skin and the environment everything outside of it, for much of the environment interpenetrates the organism without becoming a part of it. Moreover, there is an internal environment as well as an external one. Every organ, tissue or cell has its own environment in the surrounding body fluids and cells and this internal environment greatly influences the growth and development of every part. For example the development of many parts of the body depends upon internal secretions, such as enzymes or hormones, which act upon these parts as external environment acts upon the whole organism. At every stage in development the effects of external and internal environment are built into the organism and as one traces developed characters back to their earliest stages he realizes how difficult it is to separate these two sets of factors. And yet such a separation is at least *ideally* possible at every stage. We may say that the protoplasm represents the organismal factor, the non-protoplasmic substances the environmental. Possibly even protoplasm may be analyzed into a stimulating and a reacting portion, into environmental and formative substances, and this is indeed the view to which recent studies on the cellular basis of heredity have come. According to this view the protoplasm of the germ cells is not all equally concerned in inheritance, but a small portion of these cells, the chromatin, represents the hereditary organization, while the remaining portions act as innermost environment to this innermost organization. So far at least there is an actual basis in observation and experiment for separating hereditary and environmental factors, intrinsic and extrinsic causes, but whether such analyses can be extended to the different substances of which the chromatin is composed is at present unknown.

In this analysis into outer, inner and innermost environment and organization what are the distinguishing marks of the two sets of factors at every stage? Is it not that the intrinsic factor is in every instance the more specific one? In the same dish of water one egg will develop into a fish and another into a frog; the environment being the same in the two cases, the different results must be due to differences in the two eggs. Bathed in the same body fluids, one cell develops into muscle and another into nerve, owing to initial differences in the two cells. The same internal secretion in the blood affects different kinds of cells and different parts of the body differently, thus the internal secretion of the sex gland leads to the development of the most diverse secondary sexual characters in different parts of the body, depending upon the specific nature of the cells acted upon. Within a single cell different chromosomes have different peculiarities both of structure and function; one may be short, another long; one may be a factor in determining sex another in determining color, etc., and yet all of these chromosomes are surrounded by a common cell substance and are bathed in common fluids. In each of these instances both intrinsic and extrinsic factors are indispensable and practically inseparable, but the intrinsic factors are more specific than the extrinsic ones.

(2) *Structure and Function.*—As environment may be analyzed into outer and inner, so for convenience and effectiveness of treatment organisms may be studied from the standpoint of their structures or their functions, but a living thing consists of both structures and functions and in reality these can not be separated from one another. Failure to recognize this is due perhaps to the fact that after the death of an organism its functions cease to exist, but its grosser structures, especially those composed of non-living or formed material, persist for a time and are often referred to as if they constituted the whole organism. But the active, living structure is the formative material or protoplasm of the cells and it is certain that the structure of this is not the same in the living and in the lifeless condition. Confusion on this subject would be avoided if, instead of thinking of the structures of organisms or of organs as a whole, composed as they are of much formed material as well as of protoplasm, we should have in mind the structures and functions of the living substance only. As long as life lasts the structures and functions of protoplasm are both present and inseparable; neither functionless living structures nor disembodied functions exist in organisms.[3] A living thing is a system in action; it is matter and energy. When the action wholly ceases the system is dead; when the contained energy is liberated from coal or from protoplasm the remaining matter ceases to be coal or protoplasm. Function and structure are two aspects of one thing, namely, life; they are the obverse and reverse sides of the same coin.

It would be unnecessary to mention these very elementary truths were it not for the fact that so many persons have failed to appreciate their significance. From the time of Aristotle and Plato to the present many students of organisms have maintained that function is the cause of structure, as if a disembodied function could form a body around itself, as if digestion, or exertion or vision could exist apart from material bodies and then proceed to form a stomach or kidney or eye. Lamarckians generally hold that modifications of functions or habits cause modifications of structures, as if the change in function preceded the change in structure. But there is good reason to believe that every change in function is accompanied by a corresponding change in structure, and *vice versa*. Because of the fact that functional changes are more easily seen than structural ones a change of function may occur without any visible change of structure; but this merely means that physiological indicators are more delicate than morphological ones. We know, for example, that there are actual structural differences between the egg of a worm and that of a starfish, but these structural differences were not discovered until very recently, whereas the differences in the developmental functions of these two eggs have been known from the first. There are many bacteria which can be distinguished only by their functions; for example one will liquefy agar, another will not, one will ferment dextrose another levulose, etc., and yet there is no reason to doubt that there are corresponding structural differences between these forms which have not yet been seen. Different chemical substances are often recognizable only by their reactions and yet every molecule probably has its distinctive structure.

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[3] Rudimentary organs or structures may seem to negative this statement, but while such structures may lose or change their original functions they can never be said to have no function.

To attribute growth, differentiation or evolution to function rather than to structure is due merely to lack of clear thinking. No doubt functional activity is a most important factor in growth and development; the used muscle grows in size and power, the unused one remains undeveloped or even atrophies. But in the use of a muscle both structure and function are involved; some *thing*, some *structure* contracts and as a result receives increased nutriment, and there is coincident growth both of structure and function. The long neck of the giraffe has been attributed to its habit of browsing on trees, the long neck of the clam to its habit of deep burial in the mud. It is pertinent to inquire where these animals got these habits and indeed what habit consists in and whether changes of habits may occur without corresponding, though perhaps very minute, changes of structure.

On the other hand the morphological view of development and evolution regards structure as preceding function; changes in function or habit are held to be caused by changes in structure. This opinion was once widely prevalent among morphologists and yet it has no more foundation in fact than the opposite view; the fact is that both the functional and the structural views of development and of evolution are partial views caused by a too narrow consideration of organisms from one or the other standpoint. So far as we know neither function nor structure stands in a fixed *causal* relation to the other though each conditions the other. Instead then of maintaining as most evolutionists have done that function is the cause of structure or that structure is the cause of function, the biologist who can see life and see it whole recognizes that neither of these aspects of an organism can exist by itself and that neither is the cause of the other. Function is not primary and structure secondary, but both change and evolve together.